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A REVISION OF *ARABELLA MUTANS* (CHAMBERLIN, 1919) AND RELATED SPECIES (POLYCHAETA: ARABELLIDAE)

G. Kent Colbath

Abstract.—*Arabella mutans* (Chamberlin, 1919), previously considered circumtropical in distribution, is revised using a combination of soft-part, setal, and maxillary characters. Emphasis is placed on adopting a population approach to evaluating character states. Poorly preserved, isolated, or juvenile individuals may not be identifiable to species based on the criteria advocated here. Seven species with non-overlapping geographic ranges are recognized. *Arabella mutans* s. s. is restricted to tropical Polynesia. *Arabella novecrinita* Crossland, 1924 is recorded from the western Indian Ocean. *Arabella logani* Crossland, 1924 and *A. atlantica* Crossland, 1924 are recognized as distinct species, and recorded from the Red Sea and Cape Verde Islands, respectively. *Arabella multidentata* (Ehlers, 1887) is recognized to encompass western Atlantic and Carribean forms. Two new species are erected: *Arabella panamensis* for specimens from Pacific Panama, and *A. monroi* from the Galápagos.

The genus *Arabella* is distributed throughout the world ocean, and includes 20 named species (Fauchald 1977b). Many of these species are relatively rare, and have not been satisfactorily circumscribed in terms of either morphology or distribution.

Arabella mutans (Chamberlin, 1919) is one such species. Although *A. mutans* is reported to have a circumtropical distribution (Monro 1928, 1933a, b; Day 1967; Reish 1968; Gardiner 1976), this assertion has not been supported by detailed morphological comparisons of specimens (Fauchald 1970). The present study attempts to partially redress this situation by presenting information compiled from the detailed examination of numerous specimens, including the holotypes of both *A. mutans* and the similar *A. novecrinita* Crossland, 1924.

From a paleontological perspective, *Arabella mutans* is of interest because of the wide range of jaw morphologies which have been recorded for the species. Establishing constraints on the amount of variation in jaw morphology that can be expected within modern species should aid in the interpretation of fossil jaw assemblages.

History of Study

Chamberlin (1919:329–332) described the new genus and species *Cenothrix mutans* based on a single specimen collected from Easter Island by the Albatross Expedition. He distinguished the genus *Cenothrix* from *Arabella* Grube, 1850 on the presence of a ventral, hooded seta in medial and posterior parapodia in the former, and the supposed absence of such setae in the latter. The new species was distinguished on the same taxonomic character.

Crossland (1924:70) considered the presence of a single hooded seta per parapodium insufficient grounds for recognition of a new genus, and transferred *C. mutans* into *Arabella*. He described the new species *Arabella novecrinita* based on 16 specimens from the Atlantic and Indian Oceans, and noted that *A. novecrinita* ". . . is like, and probably identical with *A.* (*Cenothrix*) *mu-*

tans," (Crossland 1924:71). Crossland apparently considered the jaws of the type specimen of *A. mutans* atypical, and justified the erection of a new species on that basis. He recognized four varieties of *A. novecrinita*: the type material from Zanzibar and the Maldive Islands, *A. novecrinita* var. *logani* from the Red Sea, and *A. n.* var. *atlantica* and *A. n.* var. *asymmetrica* from the Cape Verde Islands.

Monro (1928:91; 1933b:88) considered *A. novecrinita* a junior synonym of *A. mutans,* and considered the species circumtropical in distribution. Monro essentially used Chamberlin's specific name for specimens included within the range of variation described by Crossland. Subsequent workers prior to Orensanz (1974) followed Monro, although Fauchald (1970:129) noted that Monro's revision did not involve examination of the type material of either species, and suggested that *A. mutans,* as considered by Monro, might actually include several species with more restricted distributions.

Orensanz (1974:388) used *Cenothrix* as a subgenus of *Arabella,* and recognized three species within the subgenus, which he distinguished based on their maxillary morphology. *A. mutans* was recognized for specimens with asymmetrical maxillae with falcate MI elements, *A. asymmetrica* for those with asymmetrical maxillae with a bifid left MI, and *A. novecrinita* for those with symmetrical maxillae.

Perkins (1979:445–450) followed this arrangement and placed three species in *Arabella* (*Cenothrix*). He made the important observation that the type specimens of both *Arabella multidentata* (Ehlers, 1887) and *A. maculosa* Verrill, 1900 have "hooded" ventral setae, and therefore should not be considered junior synonyms of *Arabella iricolor* (Montagu, 1804) as proposed by Hartman (1944:173). Perkins distinguished *A. multidentata* from *A. mutans* based on jaw symmetry, and considered the two species sympatric in the Florida region. He recognized *A. maculosa* based on the extreme asymmetry of the "hoods" on the ventral setae on the type specimen from Bermuda.

Materials and Methods

The extensive collection of specimens catalogued as *Arabella mutans* in the U.S. National Museum of Natural History (USNM) was examined in its entirety, as were samples identified as *Arabella novecrinita.* Additional material was obtained from the British Museum (Natural History) (=ZK), including Crossland's type material for *A. novecrinita.* Selected specimens of *Arabella iricolor* from the National Museum collection and the Florida Department of Natural Resources (FSBC, EJ) were also examined for comparative purposes.

On each dissected specimen the lengths of the first maxillae (MIs), length and width of the prostomium, and length of the peristomium were measured. Measurements were made using an ocular micrometer on a Wild M5 wide-field microscope. Denticles were counted (where possible) for all maxillary jaws.

Setae were prepared for scanning electron microscopy by allowing parapodia suspended in alcohol to dry onto glass cover slips, which were in turn glued onto stubs. Jaws were mounted by leaving a flange of muscle tissue around the jaw margins which, when dried, fixed the jaws firmly onto glass cover slips. All specimens were coated with a thin film of carbon, then sputter coated with gold palladium. Observations were made on a Cambridge scanning electron microscope at the National Museum of Natural History, Smithsonian Institution.

Taxonomic Characters

Arabella mutans has been recognized by most authors based on the presence of a single morphologic character (the "hooded" ventral seta). Consideration of additional characters coupled with a closer examina-

Table 1.—Distribution of taxonomic characters in species of *Arabella* under consideration.

Species	Nuchal papillae	Anal cirri	Postsetal lobe	Ventral setae	Maxillary symmetry	Robust MI
iricolor	no	2	short	ridged, gradual	invariant	bifid-falcate
atlantica	no	?	short	ridged, abrupt	invariant	falcate
logani	no	0	short	ridged, gradual	?	absent
monroi	no	0	short	ridged, abrupt	invariant	falcate
multidentata	no	4	short	ridged, abrupt	polymorphic	bifid
mutans	no	4	short	smooth, abrupt	polymorphic	dentate
novecrinita	no	4	short	smooth, abrupt	invariant	absent
panamensis	no	2	long	ridged, abrupt	polymorphic	falcate
sp. A	yes	?	short	ridged, abrupt	polymorphic	bifid

tion of the setae has allowed separation of discrete morphological subgroups, here recognized as distinct species with discrete geographic ranges. The taxonomic characters are discussed below, and the character states exhibited by each of the species are listed in Table 1.

Soft-part morphology.—Soft-part morphology within the genus *Arabella* is notoriously uniform and relatively simple, which accounts in part for the difficulty encountered in treating these worms taxonomically. The relative proportions of the prostomium are fairly uniform throughout the *A. mutans* species complex, and the ventral furrowing of the peristomium, although variable, does not seem to vary in a systematic fashion.

There are three features which are useful in differentiating these species, however. The postsetal lobe in parapodia from *A. panamensis,* n. sp. is markedly longer than that in the other species.

Nuchal papillae are present in some large individuals from Guayanilla Bay, Puerto Rico, a unique feature in the arabellids. The specimens are from a population of otherwise identical worms which lack papillae, however, and the taxonomic significance of this character is unclear.

The morphology of the pygidium is an extremely useful character, limited only by the difficulty of obtaining complete specimens. Species are characterized by having two anal cirri (Fig. 3b, f), four anal cirri (Fig. 3c, d), or two swollen pads lacking cirri (Fig. 3a, e).

Setae.—The most important point to emerge from SEM examination of the setae from the specimens studied here is that the "hooded" ventral seta in medial and posterior parapodia used to define *A. mutans* is not hooded (in the sense of having a three dimensional structure enclosing the distal end of the seta). In all specimens examined, the distal end of the ventral seta consists of a relatively flat extension of the setal shaft.

Although the diameter of the ventral seta is generally twice that of the other setae in these forms, it originates in the same muscular bundle, and is not an acicula as recorded by some authors. The modification of the distal end of the ventral seta is different only in degree, not in structure, from that observed in the ventral setae of *Arabella iricolor.* This observation strongly supports Crossland's (1924) contention that *Cenothrix* Chamberlin should be regarded as a junior synonym of *Arabella.*

The terminology adopted here to describe the ventral setae is illustrated in Fig. 1. Three distinct morphologies are recognized. The shaft of the seta may be smooth with an abrupt taper from the shaft to the guard, ridged with an abrupt taper from the shaft to the guard, or ridged with a gradual taper

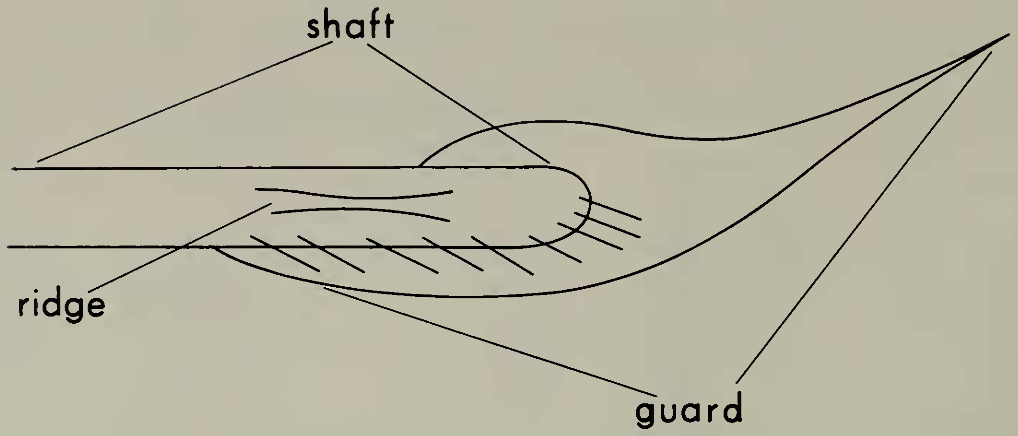

Fig. 1. Terminology used to describe morphology of the ventral seta in medial and posterior parapodia.

from the shaft to the guard. *Arabella panamensis,* n. sp. has ventral setae which are somewhat modified from the second type above in having an additional ridge near the tip of the shaft (Fig. 3h).

SEM examination of the other setae reveals that the distinction between smooth and "toothed" geniculate setae made by both Chamberlin (1919) and Crossland (1924) is indeed significant. The "toothed" setae are not actually toothed, however, but are instead ringed with loose rows of large fibrils, in contrast to the tight, irregular arrangement of fibrils in the smooth setae (Fig. 4k, l).

Jaws.—Maxillary jaws in eunicoid polychaetes are numbered, by convention, from posterior to anterior with roman numerals. Left and right jaws are indicated by a capital L or R respectively. Thus MIR refers to the posterior maxilla on the right side of the apparatus. Denticle formulas are indicated in sequence, with the left jaw in a given pair listed first. For populations, the low end of the range of denticles for a given jaw is listed first, with the high end of the range in parentheses.

Maxillae within some of the species are here considered polymorphic, but variation within single populations is limited to two or three morphs. The first and second maxillae (MI and MII) were found to be the most significant in differentiating species. The morphs recognized here are illustrated in Fig. 2. The MII jaws may be either "long," extending posteriorly to the base of the MI, or "short," extending posteriorly only half of the distance to the base of the MI (Fig. 2a, b). A long MII is invariably associated with a relatively slender MI (here termed "gracile") with a single falx (or hook) and a pronounced gap between the falx and the basal denticle row (Fig. 2e). MIs adjacent to short MIIs are wider and generally slightly longer than the gracile MIs, and are here termed "robust." They may take one of three forms in adult worms. These jaws may have a single falx with pronounced gap (="falcate," Fig. 2c), a bifid falx with pronounced gap (="bifid," Fig. 2d), or no distinct falx and no gap (="dentate," Fig. 2f). Dentate MIs are found in juvenile specimens of a number of different species, but in the juveniles with dentate MIs the anterior denticles project laterally rather than dorsally as in the adults (compare Fig. 4c, d).

The statistical frequency of these jaw morphologies varies systematically among different populations of worms, and in most cases only one of the three morphologies of robust MIs is represented (if any). The presence or absence of jaw symmetry polymorphism within a population is also a useful taxonomic character.

Within the species considered here, the lengths of MIs are highly correlated with the sizes of individual worms as measured by prostomial width (Fig. 7). A plot of MI length against prostomial width is similar for most of these species, with the exception of *Ar-*

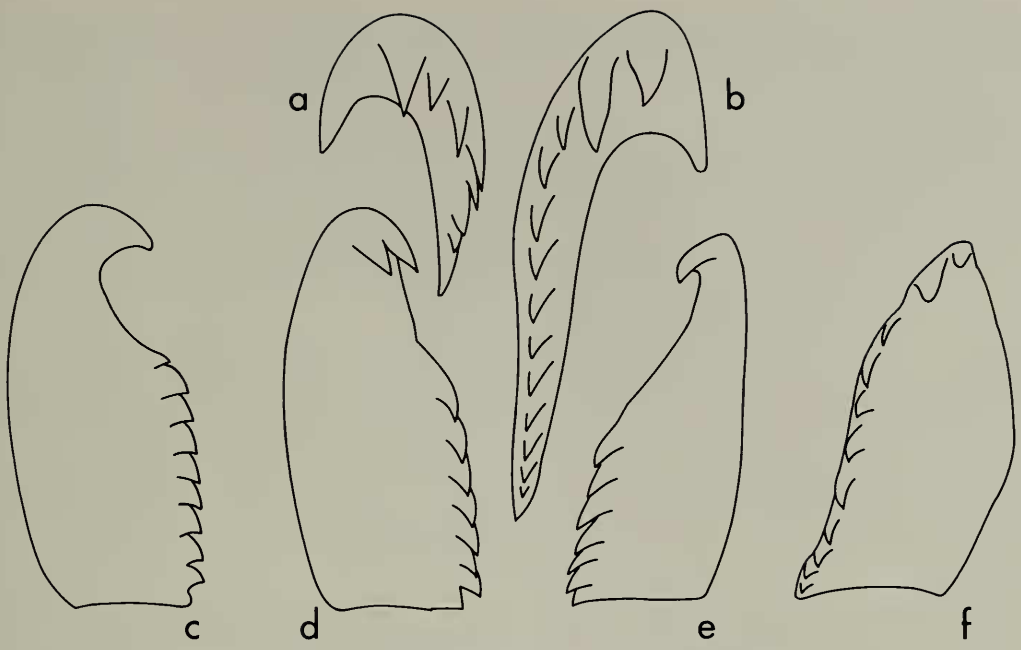

Fig. 2. Schematic representation of morphologies observed in first and second maxillae. a, short MII; b, long MII; c, falcate robust MI; d, bifid robust MI; e, gracile falcate MI; f, dentate robust MI.

abella panamensis. In *A. panamensis* individuals have relatively large jaws for their size.

The number of denticles on a given maxilla is variable, and has generally been discounted as a useful taxonomic character in eunicoid polychaetes (Kielan-Jaworowska 1966, Wolf 1980). With sufficient specimens, however, it may be possible to use the number of denticles on a statistical basis (see below under *Arabella multidentata*).

The shape of the mandibles exhibits within-sample variation in these forms (Crossland 1924), but proved of no value in distinguishing species. A typical mandible is illustrated in Fig. 5b.

Order Eunicida Fauchald, 1977
Family Arabellidae Hartman, 1944
Genus *Arabella* Grube, 1850

Arabella Grube, 1850:17.
Notopsilus Ehlers, 1868:406.
Maclovia Grube, 1871:58.
Cenothrix Chamberlin, 1919:329.

Type species.—*Arabella iricolor* (Montagu, 1804).

Remarks.—Fauchald (1977b:110–11) noted that generic diagnoses within the Arabellidae are inconsistent. In forms with projecting acicular spines, the shape of the MI is used to separate the genus *Drilonereis* Claparede (falcate MIs) from *Notocirrus* Schmarda (dentate MIs), while the genus *Arabella* (which lacks emergent acicular spines) includes forms with both maxillary morphologies. Fauchald suggested that either the genus *Notopsilus* Ehlers be recognized to include species with dentate MIs which are presently placed in *Arabella,* or that *Drilonereis* and *Notocirrus* be considered synonymous.

The report here of species in which the jaws are polymorphic (including both dentate and falcate MIs) strongly suggests that *Notopsilus* should be considered a junior synonym of *Arabella.* This does not imply, however, that *Drilonereis* and *Notocirrus* should also be considered synonymous. The basic arrangement of jaws is quite different in *Drilonereis* than it is in *Notocirrus,* and intermediate or hybrid maxillae have not been recorded.

Arabella iricolor (Montagu, 1804)
Figs. 3b, 4j, k, 5a, 6a

Nereis iricolor Montagu, 1804.
Arabella iricolor.—Pettibone, 1963:269, fig.

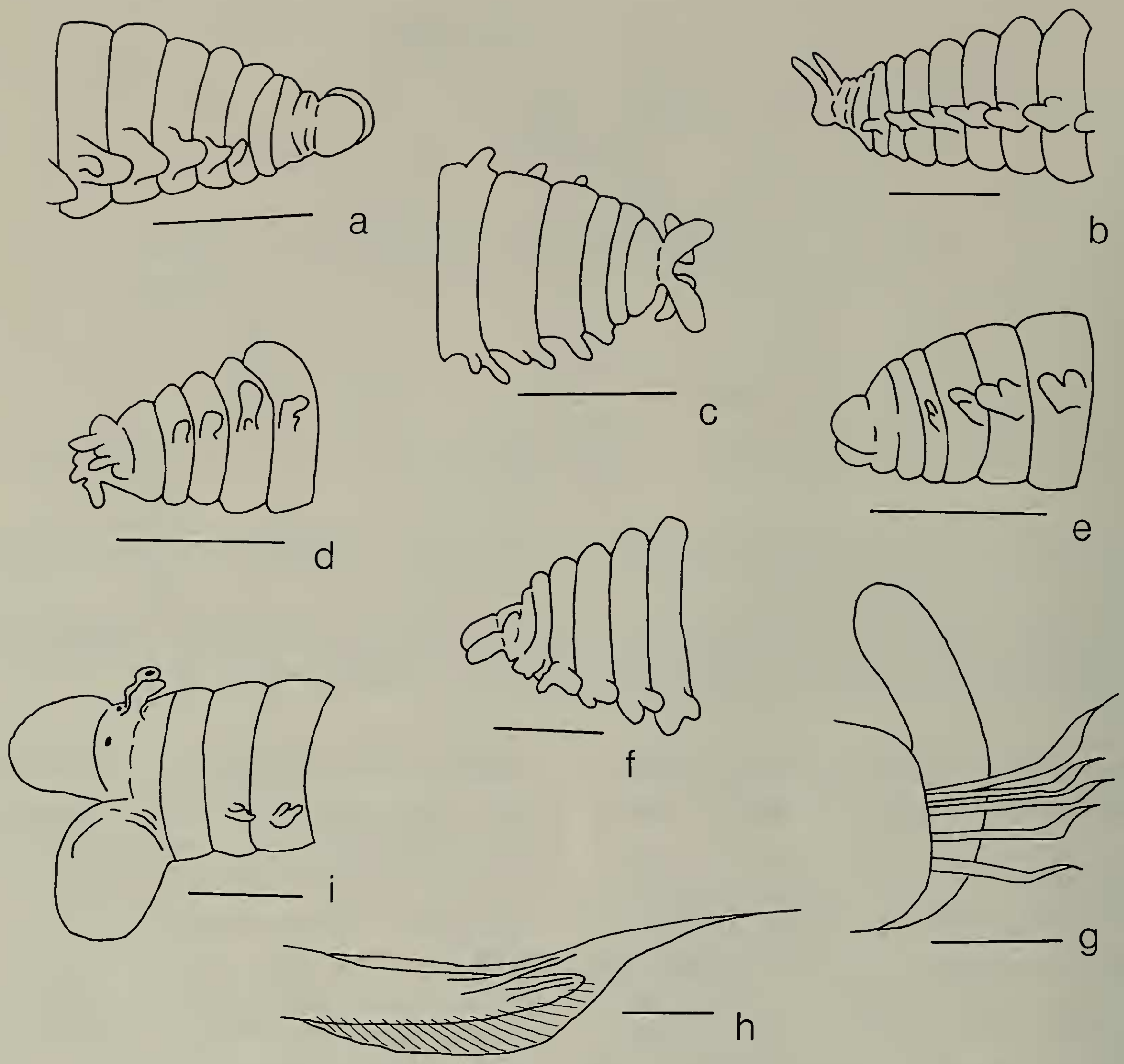

Fig. 3. a, *Arabella logani,* holotype, ZK 1924.3.1.15, pygidium, left-lateral view; b, *Arabella iricolor,* USNM 61732, pygidium, right-lateral view; c, *Arabella novecrinita,* lectotype, ZK 1924.3.1.15, pygidium, dorsal view; d, *Arabella mutans,* USNM 57434, pygidium, oblique right-lateral view; e, *Arabella monroi,* holotype, ZK 1932.12.24.595, pygidium, right-lateral view; f–h, *Arabella panamensis,* USNM 98237, holotype; f, pygidium, dorsal oblique right-lateral view; g, posterior parapodium, anterior view, note elongate post-setal lobe; h, ventral seta of parapodium in g, note 2 ridges, abrupt taper of shaft; i, *Arabella* sp. A, USNM 54915, anterior end with pharynx extended, lateral view, note nuchal papillae. Scale bars on a–f, i = 0.5 mm; g = 0.2 mm; h = 20 μm.

71a–e; Gardiner, 1976:206–207, figs. 27r–u, 28a; Uebelacker, 1984:42–5, fig. 42–2.

Materials examined.—USNM 30058, FSBC I 24159, Seashore Key, Florida (6); FSBC I 13436, Terra Ceia Bay, Florida (1).—FSBC I 13102, Lower Tampa Bay, Florida (1).—EJ-72-66, EJ-73-414, Hutchinson Island, Florida (3).—USNM 61732, USNM 53026, Cape Lookout, North Carolina (11).—USNM 4676, Woods Hole, Massachusetts (7).—USNM 33787, Provincetown, Massachusetts (8).

Remarks.—The specimens of *Arabella iricolor* examined here are characterized by having ventral setae in medial and posterior parapodia which are ridged, with a gradually tapering shaft (Fig. 4j). The pygidium has two cirri which arise dorsally (Fig. 3b). No variation in jaw symmetry was observed among adult specimens. In each individual the MIL is robust with a short MIIL, the MIR gracile with a long MIIR.

The Florida specimens differ from those from North Carolina and Massachusetts in that all adult worms have falcate robust MIs

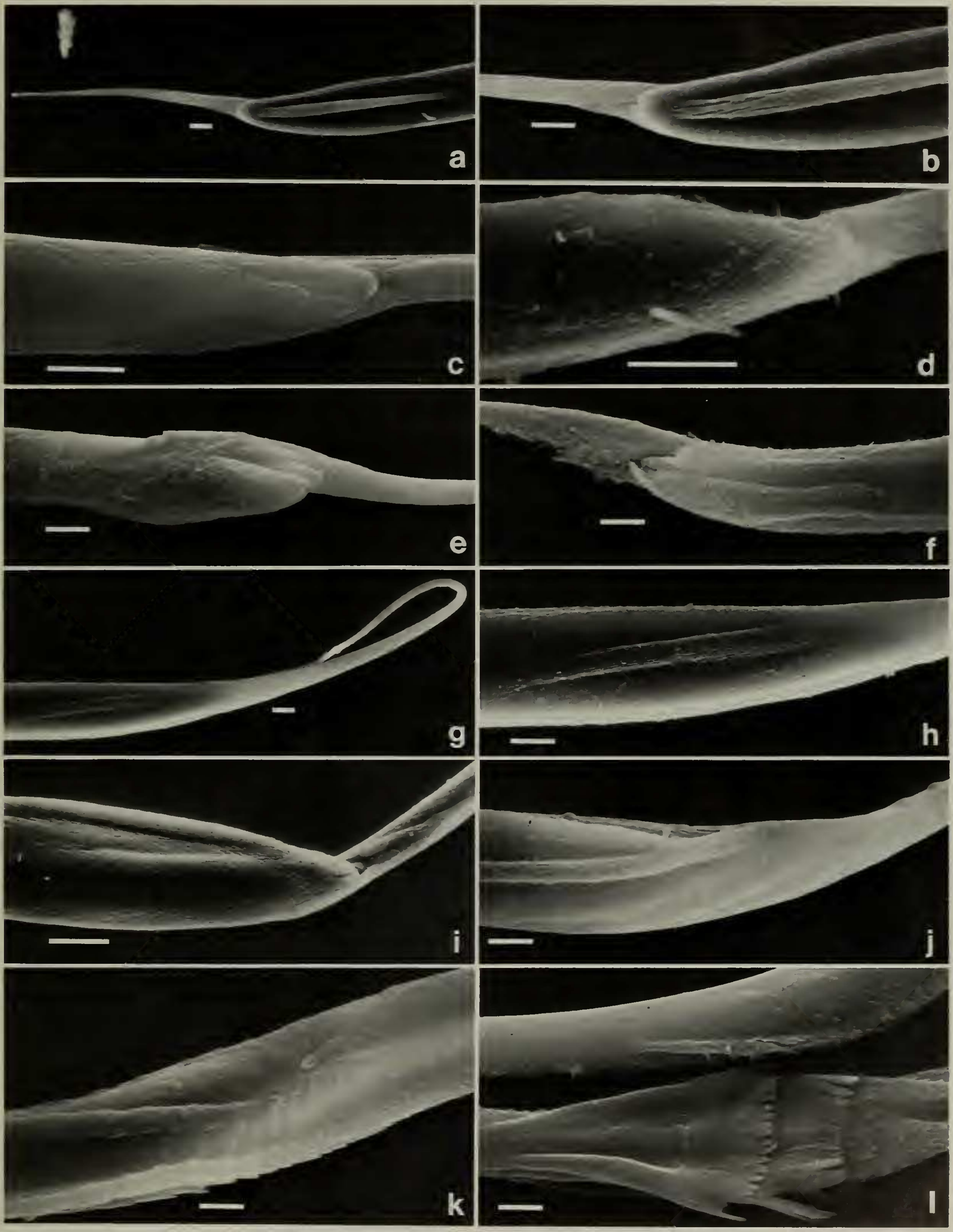

Fig. 4. Setae, all in anterior view. a, b, *Arabella monroi,* ZK 1932.12.24.337–340, paratype, large anterior fragment, ventral seta, setiger 143, note ridge, abrupt taper of shaft. c, *Arabella novecrinita,* ZK 1924.3.1.15, lectotype, ventral seta, setiger 200, note smooth, abruptly tapered shaft. d, *Arabella mutans,* USNM 23933, ventral seta, posterior setiger, note smooth, abruptly tapered shaft. e, *Arabella mutans,* USNM 57434, ventral seta, posterior setiger, dorsal to bottom of page, note smooth, abruptly tapered shaft. f, *Arabella atlantica,* ZK 1923.11.5.1–2, large syntype, ventral seta, setiger 122, note ridge, abrupt taper. g, h, *Arabella logani,* ZK 1924.3.1.15, holotype, ventral seta, setiger 125, note ridge, gradually tapered shaft. i, *Arabella multidentata,* USNM 98154, ventral seta, posterior setiger, note ridge, abruptly tapered shaft. j, k, *Arabella iricolor,* USNM 30058 (Florida); j, ventral seta, posterior setiger, note ridge, gradually tapered shaft; k, "smooth" seta, posterior setiger. l, *Arabella* sp. A, USNM 54915, posterior setiger, smooth seta above, toothed seta below. All scale bars = 5 μm.

(n = 8), in contrast to the bifid robust morphology (Fig. 5a) observed in the northern populations (25 of 26 adult specimens).

Jaw morphology in these populations is quite stable, as the jaws are essentially identical in specimens collected from Woods Hole in 1883 (USNM 4676), Provincetown in 1954 (USNM 33787), and North Carolina in 1974 (USNM 53026) and 1975 (USNM 61732). Thus although the difference between the Florida and northern populations is small, the stability of the character suggests that the difference is hereditary, and may be used to subdivide east coast populations of *A. iricolor.* As presently recognized, *A. iricolor* is probably a species complex.

Two juvenile specimens of *A. iricolor* from Florida have dentate MILs which resemble those in several other species of *Arabella,* including *A. mutans* (Fig. 5d).

Arabella atlantica Crossland, 1924, new rank
Fig. 4f

Arabella novecrinita var. *atlantica* Crossland, 1924:78–80, text-figs. 99–101, 105.
Arabella novecrinita var. *asymmetrica* Crossland, 1924:80–83, text-figs. 102–104.

Syntypes.—ZK 1923.11.5.1-2, Cape Verde Islands, two anterior fragments.

Materials examined.—ZK 1923.11.5.1–2, Cape Verde Islands (two anterior fragments).—jaw mounts from six specimens from the Cape Verde Islands as follows: ZK 1923.11.8.12–14, three unregistered slides labelled CV Isl. W9; three unregistered jaw mounts of *Arabella novecrinita* var. *asymmetrica,* Cape Verde Islands.

Remarks.—Crossland (1924:78) recorded 11 specimens from the Cape Verde Islands. Three small specimens which exhibit maxillae typical of juveniles in the genus *Arabella* were assigned to *Arabella novecrinita* var. *asymmetrica* (Crossland, 1924, text-fig. 103). These specimens are here regarded as juveniles of *Arabella atlantica.*

Of the remaining eight specimens, two anterior fragments and six sets of jaws are represented in the collection of the British Museum (Natural History). At present it is impossible to determine which sets of jaws belong to the two preserved specimens, and thus no lectotype is designated.

The soft-part morphology of this species is adequately described by Crossland (1924: 78–80, text-fig. 99). The ventral setae are ridged, with an abrupt taper from the guard to the shaft (Fig. 4f). In the specimens available for examination, the MIL is robust falcate, the MIIL short, and the MIR gracile falcate with a long MIIR. No symmetry polymorphism observed (n = 6).

This species is distinguished from *Arabella novecrinita* by its ridged ventral setae and robust MIL. It differs from *A. multidentata* in having falcate rather than bifid robust MIs, and in not exhibiting symmetry polymorphism. *A. atlantica* most closely resembles *A. monroi* n. sp. from the Galápagos, but because neither preserved specimen of *A. atlantica* has an intact pygidium, it cannot be compared based on this important character.

Arabella logani Crossland, 1924, new rank
Figs. 3a, 4g, h

Arabella novecrinita var. *logani* Crossland, 1924:75–78, text-figs. 96–98.

Holotype.—ZK 1924.3.1.138, Red Sea.

Materials examined.—ZK 1924.3.1.138, Red Sea (1).

Remarks.—The soft-part morphology of the type and only specimen is accurately described by Crossland (1924:75–76). Noteworthy is the presence of two inflated pads on the pygidium (Fig. 3a) which lack anal cirri. No evidence for incomplete regeneration is apparent, and this may represent the fully developed character state.

The ventral setae in posterior parapodia

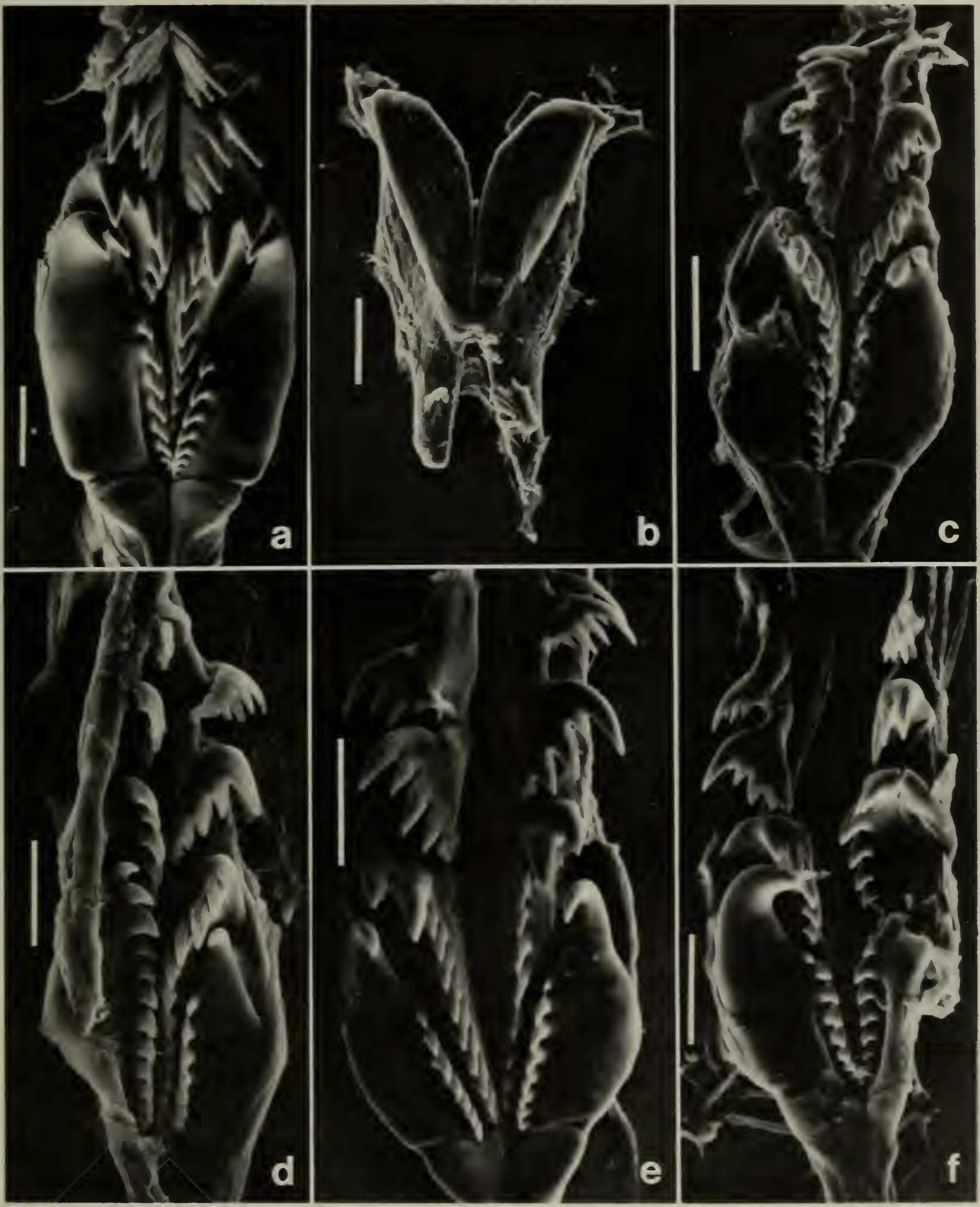

Fig. 5. a, *Arabella iricolor,* USNM 33787, maxillae, dorsal view, note bifid MIL. b–d, *Arabella mutans,* USNM 23933; b, mandibles, ventral view; c, maxillae of adult specimen, dorsal view, note dentate MIR, falcate tip of MIL broken during mounting; d, maxillae of juvenile specimen, note dentate MIL with anterior denticles which project laterally. e, *Arabella* sp. A, USNM 54915, maxillae, dorsal view, example of symmetrical apparatus with 2 long MIIs, 2 gracile falcate MIs. f, *Arabella panamensis,* USNM 66043, paratype, maxillae, dorsal view, note falcate MIL, falcate tip of MIR broken during mounting. Scale bars on a–c, e, f = 100 μm; d = 50 μm.

are ridged and gradually tapering (Fig. 4g, h), and are thus unlike those in other species within the *Arabella mutans* complex.

The MIL is robust bifid, the MIIL short, and the MIR gracile falcate with a long MIIR (note that Crossland reversed the image in text-fig. 96, and incorrectly labeled the specimen as a "Cape Verde specimen"). The bifid MIL serves to distinguish this species from *Arabella iricolor,* which in the eastern Mediterranean and Red Sea has a falcate robust MIL (Ben-Eliahu 1976:172). No statement concerning jaw variability can be made based on a single specimen, and full characterization of the species must await further collecting.

Arabella monroi, new species

Figs. 3e, 4a, b

Arabella mutans.—Monro 1933b:88–89 (in part).

Holotype.—ZK 1932.12.24.595, washed from peat, Isla Santa Cruz (Indefatigable), Galápagos Islands.

Etymology.—In honor of C. C. A. Monro.

Materials examined.—Holotype; ZK 1932.12.337–340 (paratypes), washed from peat, Isla Santa Cruz (Indefatigable), Galápagos Islands (26).—ZK 1932.12.336, fine gravel in pools, Isla Isabela (Albermarle), Galápagos Islands (1).—ZK 1932.12.341, Post Office Bay, Isla Santa Maria (Charles), Galápagos Islands (3).

Description.—Prostomium bullet-shaped, slightly longer than wide to slightly wider than long, V-shaped furrow on ventral surface, four eyes embedded in posterior dorsal margin. Peristomium divided into two rings, a shallow ventral median furrow in anterior ring only.

Setigers numerous, exceeding 200 in large, adult specimens. Notopodia represented by small tubercle, neuropodia with blunt, subtriangular postsetal lobe. Pygidium with two swollen pads (Fig. 3e), no anal cirri observed.

Notoacicula small, 2–3 per setiger. Neuroacicula large, amber colored, 3–4 per setiger with tips protruding slightly through parapodial wall. Anterior setigers with 5–6 setae, 3 being smooth, 2–3 toothed. Medial and posterior setigers with 2 smooth, 1 toothed, and 1 ventral seta. Ventral setae ridged, shaft tapering abruptly to distal guard (Fig. 4a, b).

Mandibles H-shaped, typical of *Arabella.* Maxillae with 2 long carriers and unpaired ventral ligament (="third carrier" of some authors). Maxillary apparatus asymmetrical, no symmetry polymorphism observed. MIL robust falcate, MIIL short, MIR gracile falcate, MIIR long. Denticle formula: 6(9)-6(8); 7(8)-12(16); 5(6)-5(6); 4(5)-4; 1-1.

Holotype large, complete individual with 208 setigers, prostomium 0.68 mm long, 0.55 mm wide, peristomium 0.54 mm long, MIL 0.36 mm long, MIR 0.35 mm long, denticle formula 9-8; 8-16; 6-6; 4-4; 1-1.

Remarks.—The collection from the Galápagos includes 13 complete specimens. None have anal cirri, and it seems likely that the presence of two pygidial lobes with no cirri represents the fully developed adult character state.

Arabella monroi is distinguished from *A. mutans* based on its asymmetrical maxillae which are not polymorphic, falcate rather than dentate robust MIs, ridged rather than smooth ventral setae, and by the absence of anal cirri. It differs from *A. multidentata* in having falcate rather than bifid robust MIs, in not exhibiting symmetry polymorphism of the maxillae, and in lacking anal cirri.

The maxillary apparatus in *A. monroi* is identical to that in *A. atlantica.* The pygidium in the latter species is unknown, however, and I consider it prudent to describe the Galápagos specimens as a separate species pending collection of additional material from the type locality of *A. atlantica.*

The geographic range of *A. monroi* is presently restricted to the islands of the Galápagos.

Arabella multidentata (Ehlers, 1887)
Figs. 4i, 6b, 7

Aracoda multidentata Ehlers, 1887:112, pl. 34, figs. 8–10, pl. 35, figs. 1–4.
Arabella multidentata.—Hartman, 1938:12; Perkins, 1979:447–449, fig. 13; Uebelacker, 1984:42–9, figs. 42–5, 6a–g.
Arabella maculosa Verrill, 1900:651.—Treadwell, 1921:114, pl. 9, figs. 12–13, text-figs. 424–428; Perkins, 1979:450, fig. 14.
Arabella mutans.—Gardiner, 1976:206, figs. 27o–q; Fauchald, 1977a:45 (in part); Perkins, 1979:445–447, fig. 12; ?Dueñas, 1981:193.
Arabella novecrinita.—Monro, 1933a:260–261.
?*Arabella asymmetrica.*—Orensanz, 1974: 368–388, fig. III-6.

Holotype.—MCZ 825, Florida.

Materials examined.—USNM 55882, Gulf of Mexico (1).—USNM 54694–54696, Hutchinson Island, Florida (3).—USNM 59526, N Atlantic off Florida (2); USNM 59528, N Atlantic off N Carolina (1).—USNM 56844, N Atlantic off Virginia (1).—USNM 98142–98156, Bermuda (22).—USNM 53297, 54215, 54220, 54221, 54223, 54818, 54820, 98238, Guayanilla Bay, Puerto Rico (22).—USNM 54217, 54218, 54222, 54837–54840, Jobos Bay, Puerto Rico (8).—USNM 66044–66046, 73653, Galeta Reef, Panama (5).—?USNM 58273, Bay of Cartagena, Colombia (1).

Remarks.—Perkins (1979:448–449) accurately described the soft-part morphology of *A. multidentata.* To his description of the setae I add that the ventral setae are ridged and abruptly tapered (Fig. 4i).

Perkins (1979:450) distinguished *Arabella maculosa* Verrill, 1900 from *A. multidentata* based on the "more obviously asymmetrical" ventral setae in the syntype of the former. I found the degree of asymmetry variable on a single specimen, and was unable to separate the species on this basis. The syntype of *A. maculosa* has a regenerated pygidium with two poorly developed lobes and no cirri (Perkins 1979, fig. 14a). Eight complete specimens from Bermuda, with no indication of posterior regeneration, have four anal cirri as is typical of *A. multidentata.* The jaws of the Bermuda specimens are indistinguishable from those of other west Atlantic and Caribbean populations of *A. multidentata* (Table 2), and I therefore consider *A. maculosa* a junior synonym of *A. multidentata.*

Table 2.—Distribution of specimens of *Arabella* with particular MI morphologies in polymorphic species.

Species	2 robust	1 gracile, 1 robust	2 gracile
multidentata			
Bermuda	1	9	8
Others	3	15	12
mutans	4	4	2
panamensis	3	5	—
sp. A	—	4	2

Perkins (1979:447) distinguished sympatric Florida populations of *A. multidentata* from *A. mutans* based on jaw symmetry. Instead, I recognize a single species (*A. multidentata*) with polymorphic jaw symmetry which is distinct from *A. mutans.* *A. multidentata* has bifid (25 of 27 adult specimens with robust elements, remaining 2 falcate) rather than dentate robust MI elements (where present), and further differs from *A. mutans* in having ridged rather than smooth ventral setae.

A comparison between *A. multidentata* and *A. iricolor* sensu Pettibone (1963) is particularly instructive, as the geographic ranges of the two species overlap along the east coast of the United States. *A. multidentata* has abruptly tapering shafts on the ventral setae (Fig. 4i), rather than gradually tapering shafts as in *A. iricolor* (Fig. 4j), is further characterized by having four rather than two anal cirri, and by having polymorphic maxillary symmetry. The number of denticles

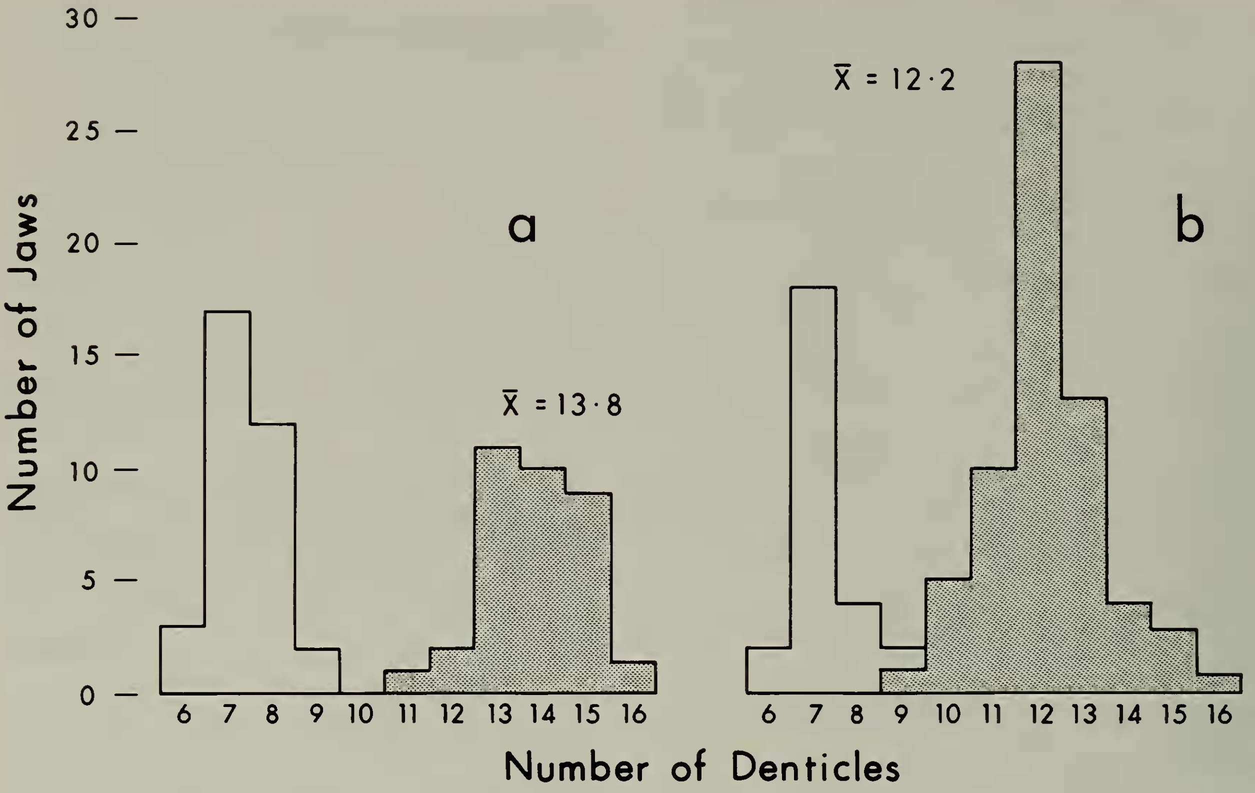

Fig. 6. Histograms of denticle number in MII jaws in *Arabella iricolor* (a) and *Arabella multidentata* (b). Note that the distinction between short and long MII elements is evident from the diagram. Means are indicated for long MIIs.

in long MII elements overlaps between the two species (Fig. 6a, b), but the difference in means is highly significant ($P < 0.001$, $t = 6.14$).

Dentate jaws were observed in four juvenile specimens of *A. multidentata.* The juvenile dentition is indistinguishable from that in other species of *Arabella.*

As defined here, *Arabella multidentata* is a west Atlantic species recorded from the east coast of the United States as far north as Virginia, from Bermuda, Puerto Rico, the Gulf of Mexico, Atlantic Panama, and questionably from the Bay of Cartagena, Colombia (single specimen with falcate rather than bifid robust MIL). The specimens described by Orensanz (1974) as *A. asymmetrica* have maxillae identical to the present material, and ventral setae with abruptly tapered shafts. It's unclear whether or not the ventral setae are ridged, however, and the pygidium was undescribed. This attribution must therefore be considered tentative.

Arabella mutans (Chamberlin, 1919)
Figs. 3d, 4d, e, 5b–d

Cenothrix mutans Chamberlin, 1919:330–332, pl. 61, figs. 2–9, pl. 62, fig. 1.
Arabella mutans.—Crossland, 1924:71; Hartman, 1954:624; Reish, 1968:220; Kohn and Lloyd, 1973:699.
Arabella novecrinita.—Hartman, 1954:625.

Holotype.—USNM 19740, Easter Island.

Materials examined.—USNM 19740, 57434, Easter Island (2).—USNM 23933–23935, Bikini Island (14).

Remarks.—Chamberlin's (1919:330, pl. 61, fig. 4) description of the anterior end of the holotype is accurate. The pygidium is poorly developed, and represents incomplete regeneration. A second specimen from Easter Island (USNM 57434) has four anal cirri (Fig. 3d), as do two specimens from Bikini, and this is considered the fully developed character state.

As noted above, the hooded acicula (or

"crochets") which Chamberlin (1919:331) originally described for this species are neither hooded nor acicula, but rather are setae typical of the genus *Arabella* which have an abruptly tapering shaft. The shaft is smooth on ventral setae in the holotype, and on the other specimens examined (Fig. 4d, e).

Chamberlin (1919:61, fig. 2) inaccurately figured the MIs in the holotype. The MIL is robust dentate, with two upturned anterior denticles (as in MIR in Fig. 5c) which were not depicted by Chamberlin. The MIR is gracile falcate with the anterior tip broken off. Examination of additional specimens reveals that maxillary symmetry is polymorphic (Table 2), and that if robust MIs are present they are dentate (Fig. 5c). Two juvenile specimens were observed with dentate MIs of the type illustrated in Fig. 5d. Mandibles (Fig. 5b) are as described by Chamberlin (1919:332, pl. 61, fig. 3).

Arabella mutans most closely resembles *A. novecrinita* as restricted here. In contrast to the symmetry polymorphism exhibited by *A. mutans, A. novecrinita* is characterized by symmetrical maxillae with gracile MIs and long MIIs. In view of the small number of *A. novecrinita* included here (n = 4), this distinction must be considered tentative. *A. mutans* has more denticles on long MIIs on average (13.3, n = 12) than does *A. novecrinita* (10.6, n = 5), but again the small sample size makes use of this distinction tentative.

As restricted here, *A. mutans* has been recorded from Easter Island and the Marshall Islands in the tropical Pacific. A specimen from Guam (USNM 54426), which had been identified as *A. mutans,* is now missing its jaws, and the identification could not be confirmed.

Day's (1975:196–197) report of *A. mutans* from Western Australia was based on a single juvenile specimen, and must be considered questionable on that basis. The jaws illustrated by Fauvel (1953:275, fig. 1401) from a small specimen collected from Ceylon are also those of a juvenile, and the record cannot be accepted. Tampi & Rangarajan (1964:11, figs. 29–31) did not describe the jaws in the anterior fragment they identified as *A. mutans* from Car Nicobar, Indian Ocean, and their record must also be considered questionable. Silva (1961:182) described but did not illustrate a specimen from Ceylon as *A. mutans* which has two "hooded acicula" per parapodium, and asymmetrical maxillae with MIL robust falcate, MIIL short, MIR gracile falcate, and MIIR long. The presence of two "hooded" setae per parapodium is unusual, and the maxillae are unlike those in either *A. mutans* or *A. novecrinita.*

Arabella novecrinita Crossland, 1924
Figs. 3c, 4c

Arabella novecrinita Crossland, 1924:71–75, text-figs. 89–95.

Lectotype.—ZK 1924.3.1.15, Zanzibar; designated herein.

Materials examined.—ZK 1924.3.1.15, Zanzibar (1).—ZK 1924.3.1.292, Minikoi Island, Maldives, mounted jaws and parapodia (1?).—uncatalogued anterior fragment, Aldabra.

Remarks.—Crossland (1924:71) recorded two specimens (with maxillary formulas) from the Maldives. The British Museum (Natural History) collection includes only mounted jaws and parapodia from this location which may be from a single specimen. In light of the fragmentary nature of the Maldive material, and the wide geographic separation between Crossland's original type localities, the Zanzibar specimen is herein designated the lectotype.

Crossland's (1924:71–75, text-fig. 89) description of the soft-part morphology in this species is accurate. Noteworthy is the presence of four anal cirri (Fig. 3c) on the lectotype (Crossland 1924:75). The ventral setae in medial and posterior parapodia have a smooth shaft which tapers abruptly to the guard (Fig. 4c). The maxillae on the lectotype are symmetrical, with gracile MIs and long MIIs (Crossland 1924:72), as are the jaws on the two specimens Crossland (1924: 73) recorded from the Maldives, and the anterior fragment recorded here from Aldabra. The jaw formula for the lectotype is 7-7; 7+-10; 5-5; 5-4; 1-1. For the species it is 6(7)-7; 10(11)-10(11); 4(6)-4(5); 4(5)-3(4); 1-1. The mandibles are typical of *Arabella,* as illustrated by Crossland (1924, text-fig. 91).

As noted above, the setae and soft-part characteristics of this species are similar to those in *Arabella mutans,* and the species are distinguished based on the maxillae.

As restricted here, *A. novecrinita* is known only from islands in the Indian Ocean. Day (1967:446, fig. 17.18f–h) recorded specimens (as *A. mutans*) from Mozambique and South Africa which may belong in *A. novecrinita* based on the illustrated maxillary apparatus. It's not clear whether the ventral setae are ridged based on Day's (1967, fig. 17.18f) illustration, and thus the report cannot be securely credited to *A. novecrinita.* A South African specimen identified as *A. mutans* in the British Museum collection (ZK 1932.11.24.38) proved to be a misidentified specimen of *Arabella iricolor* sensu lato, and thus this question remains unresolved.

Arabella panamensis, new species
Figs. 3f–g, 5f, 7

Arabella mutans.—Fauchald, 1977a:45 (in part).

Holotype.—USNM 98237, Paitilla Beach, Panama.

Etymology.—From Panama, the type locality.

Materials examined.—Holotype; USNM 66042, 66043, 66365 (paratypes), Paitilla Beach, Panama (9).—?USNM 80225, Golfo de Nicoya, Costa Rica (1).

Description.—Prostomium bullet-shaped, slightly wider than long, V-shaped mark on ventral surface, four eyes embedded in posterior dorsal margin. Peristomium divided into two rings, ventral median furrow in anterior ring only.

Setigers numerous, up to 177 in complete adults. Notopodia not expressed on surface, neuropodia with elongate postsetal lobe (Fig. 3g) which is commonly pigmented. Pygidium with two ventral anal cirri (Fig. 3f).

Notoacicula fine, from two to three per setiger. Neuroacicula large, amber colored, three per setiger, tips commonly protruding slightly through parapodial wall. Anterior setigers with three smooth and from two to three toothed setae, medial and posterior setigers with two smooth, from one to two toothed, and one ventral seta. Shafts on ventral setae taper abruptly to guard, two ridges present (Fig. 3h).

Mandibles H-shaped. Maxillae with two long carriers and unpaired ventral ligament. Maxillae exhibit symmetry polymorphism. One or both MI elements robust falcate (Fig. 5f). Denticle formula: 5(8)-6(9); 6(7) or 9-5(7) or 11(12); 4(6)-4(5); 3(4)-3(4); 1-1.

Holotype large, complete specimen with 177 setigers, prostomium 0.39 mm long, 0.70 mm wide, peristomium 0.39 mm long, MIL 0.41 mm long, MIR 0.41 mm long, denticle formula 7-9; 6-11; 6-5; 4-4; 1-1.

Remarks.—This species differs from others in the *A. mutans* complex in having longer postsetal lobes on medial and posterior parapodia, two anal cirri which arise ventrally, and in having two ridges on the ventral setae. It further differs in having somewhat longer MIs in individuals of a given size (Fig. 7). The post-setal lobe in *Arabella semimaculata* (Moore, 1911) resembles that in *A. panamensis* (compare Fig. 3g; Fauchald 1970, pl. 20, fig. g), but the former species has smoothly bilimbate ventral setae (Fauchald 1970:133), unlike the ridged, abruptly tapering ventral setae in *A. panamensis.*

A juvenile specimen from the Pacific side of Costa Rica (USNM 80225) with dentate

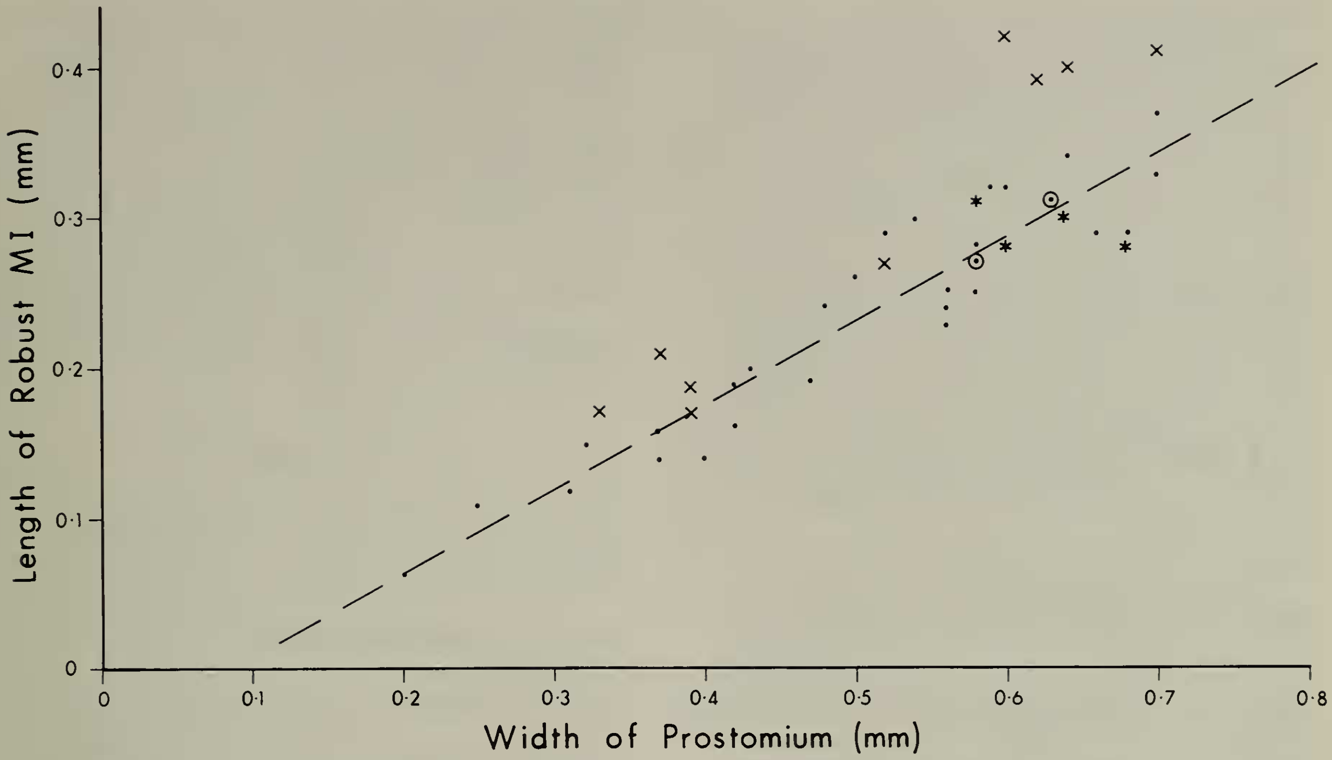

Fig. 7. Plot of robust MI length against width of prostomium for *Arabella multidentata* (●), *Arabella panamensis* (x), and *Arabella* sp. A (*). Prostomial width is less subject to distortion by fixation than is total length, and is used here as a more reliable measure of specimen size (and, by inference, maturity). The spread of points for *A. multidentata* is typical of that observed for the other species considered here with the exception of *A. panamensis.* The regression line for *A. multidentata* is of the form y = 0.55x − 0.44 (r = 0.94). Note that all of the points for *A. panamensis* plot above the regression line, suggesting that individuals of *A. panamensis* have larger jaws for their size than do individuals of *A. multidentata.* The slope of a linear regression for *A. panamensis* (not shown) is significantly different from the slope for *A. multidentata* ($P = 0.005$, $t = 3.04$, d.f. = 35). Note also that plots of points for papillate individuals (*Arabella* sp. A) fall within the large end of the range of variation for *A. multidentata.*

MIR has setae comparable to *A. panamensis,* but lacks the elongate postsetal lobe in posterior parapodia. No data is available on ontogenetic changes to be expected in this character, and the specimen is only tentatively attributed to *A. panamensis.*

The species is presently known only from the Pacific coast of Panama.

Arabella sp. A
Figs. 3i, 4l, 5e

Materials examined.—USNM 54216, 54915, 98239, Guayanilla Bay, Puerto Rico (8).

Remarks.—Three collections of *Arabella multidentata* from Guayanilla Bay included several relatively large individuals with two distinctive papillae arising from the nuchal fold (Fig. 3i). The jaws (Figs. 5e, 7) and setae are comparable to those in *A. multidentata.* No papillate specimens were recorded from any other locality, and the significance of the papillae is presently unclear. The character is sufficiently distinctive to warrant segregation of these forms (informally as sp. A) pending further investigation.

Discussion

The systematic treatment here afforded members of the *Arabella mutans* species complex should be regarded as a working hypothesis. The stability of the taxonomic characters employed can be evaluated by the collection of additional specimens, and data on additional characters (using electrophoresis, for example) can be collected for comparative purposes. Studies on the breeding interactions in living populations would, of course, provide the most powerful test of the systematics, but at the same time may be the most challenging to implement.

Particular emphasis is placed here on characterizing species based on populations rather than single individuals. Thus, polymorphism of jaw symmetry is considered a useful taxonomic character, even though it is meaningless in regard to a single individual. A single individual collected from a new location may thus not be identifiable to the species level.

This restriction especially applies to juvenile individuals. Similar maxillae have been recorded from juveniles in four (questionably five) of the species of *Arabella* considered here, although the adult maxillae in these forms exhibit significant differences.

Studies of other species of *Arabella* should consider the maturity of specimens before maxillary form is included in the species diagnosis. In particular, the distinction commonly made between *Arabella iricolor* and *A. geniculata* (Claparede, 1868) might be worth re-evaluation in this light (Fauvel 1923:439–440, fig. 175i–l; Fauchald 1970: 226; Ben-Eliahu 1976:172).

As restricted here, two of the species considered are incompletely characterized (*Arabella atlantica, A. logani*). The remaining five species are separated geographically as well as morphologically. The concept of *A. mutans* as a single circumtropical species is clearly incorrect. This observation serves to underline the futility inherent in attempting to use the distribution of rare, poorly understood species for the study of biogeography.

The chief lessons for paleontologists studying fossil polychaete jaws are as follows: 1) jaw symmetry may vary within a single population, and should be used as a taxonomic character with caution, 2) the morphologies of the MI and MII maxillary elements may be useful for species level diagnoses, 3) the denticles on jaws may be worth counting after all, but denticle number should only be used as a taxonomic character on a population basis. The second point has already been deduced from the study of fossil material (Kielan-Jaworowska 1966; Edgar 1984), suggesting that classification of recent and fossil material may be roughly comparable. The first point has been less fully appreciated, and some revision of generic and family level fossil taxa may be necessary on that basis.

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2195 Deborah Way, Upland, California 91786.